

***Wubanoides uralensis* (PAKHORUKOV 1981) – Geographic variation, mating behaviour, postembryonic development and description of a new subspecies (Araneae, Linyphiidae)**

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Abstract: An overview regarding the geographic variation of taxonomic characters is given for the linyphiid spider *Wubanoides uralensis* (PAKHORUKOV 1981). Having a distribution centre in Siberia/North Asia, it occurs only in a few disjunct, relict-like regions in Central Europe. Compared with the paratypes from the main North Asian distribution area, European specimens are taxonomically clearly distinct. Differences in habitat preference are also obvious. Hence, European populations are now being assigned to a separate taxon at subspecific level: *W. uralensis lithodytes* nov. subsp. Successful ex ovo rearings allowed detailed descriptions of postembryonic development and courtship behaviour. Additional, preliminary observations have been carried out on some ecological aspects.

Key words: Araneae, Linyphiidae, *Wubanoides uralensis*, geographic variation, new subspecies, postembryonic development, courtship behaviour.

Introduction

In 1998–99 some linyphiid spiders, belonging to the mainly Siberian genus *Wubanoides* ESKOV 1986 (ESKOV & MARUSIK 1992), were found in a block field in the Harz Mts. (Fig. 31), Lower Saxony, North-west Germany (SCHIKORA 2001). The spiders were tentatively assigned to *Wubanoides uralensis* (PAKHORUKOV 1981), since they appeared taxonomically distinct, when compared with paratypes of this species. Hitherto the only few Central European occurrences of *W. uralensis* were known from the Czech Republic (e.g. RŮŽIČKA et al. 1989, RŮŽIČKA 1990, RŮŽIČKA & ZACHARDA 1994, RŮŽIČKA 1997, RŮŽIČKA & HAJER 1996, BUCHAR & RŮŽIČKA 2002). The main distribution area of *W. uralensis* appears to be the north-east Palaearctic (North Asia sensu ESKOV 1994). Here, the species is known from West Siberia (Polar Cisuralia, northern and middle Urals, southern Urals, Yenisei), South Siberia (West Sayan, East Sayan, Tannu-Ola, Khamar-Daban and

Khentai-Nuruu mountains) and Mongolia (ESKOV & MARUSIK 1992, ESKOV 1994).

W. uralensis belongs to the rarest and most mysterious European species of spiders. Biology, ecology and distributional history have remained unknown till now. In total no more than 9 single records have been made (SCHIKORA 2001; BUCHAR & RŮŽIČKA 2002, RŮŽIČKA pers. comm.). All of them refer to extensive low mountain range block fields, where the spider exclusively inhabits the dark, deep subterranean cleft system. Since 1999 special trap types have allowed catches of living *W. uralensis* in the Harz Mountains. Even egg sacs of the spider were found attached to these traps. In the following period living specimens and egg sacs were the basis for successful ex ovo-rearings of *W. uralensis*. Improved rearing methods now permit the culturing of several generations. The description of courtship behaviour and postembryonic development of *W. uralensis* is thus one goal of this paper. The complete life cycle of a linyphiid spider,

from egg to adult, has obviously been studied only rarely. As a further goal, based on all currently available material, a first overview of the geographic variation of taxonomic characters is given.

Materials and methods

Investigated materials

Whenever juvenile spider instars are mentioned in the following, they were caught alive and reared to adulthood in captivity.

Germany: Lower Saxony, Harz Mts., Acker-Bruchberg mountain range, Altenau, quartzite block field (740 m NN).

Adults: 1 ♀ (live) 21.9.1998; 1 ♂ (live) 27.6.1999; 1 ♀ (live) 20.7.1999; 1 ♀ (live) 22.9.1999; 1 ♀ (live) 26.6.2002; 1 ♀ (live) 24.5.2003; 2 ♂♂, 1 ♀ 30.5.–27.6.1999; 1 ♀ 27.6.–3.7.1999; 1 ♂, 1 ♀ 27.6.–20.7.1999; 1 ♀ 20.7.–22.9.1999; 1 ♀ 22.9.1999 – 17.4.2000; 1 ♂ 9.7.–6.8.2001; 1 ♂, 1 ♀ 22.4.–7.6.2002; 1 ♂ 7.–26.6.2002; 1 ♀ 20.8.–20.9.2002; 1 ♀ 24.5.–13.6.2003. **Juveniles** (1st to 4th free instar): 1 ♀ 22.9.1999, 1 ♂ 24.9.2001; 3 ♂♂ 26.6.2002, 1 ♂ 20.8.2002, 2 ♂♂ 20.9.2002. **Adults from ex ovo-rearing** 1999–2002: 19 ♂♂, 26 ♀♀ (CHBS; 1 ♂, 1 ♀ CKTh; 1 ♂, 1 ♀ CVR).

Czech Republic: A) Moravia, Králicy Sněžník Mt., southern slope, 1350–1400 m NN, boulder debris, 1 ♀ 26.7.1994; B) Moravia, Jeseníky Mts., Ztracené Kameny Mt., southern part of the main crest, 1220 m NN, phyllite and quartzite block accumulations, 1 ♂, 1 ♀ 15.7.1993 – 27.7.1994; C) Bohemia, Krkonoše Mts., Sněžka Mt., western slope, mica schist taluses, 1540–1550 m NN, 1 ♂ 2.7.1988 – 26.8.1989 (leg. V. Růžička; CHBS), 1 ♂ 1.8.2003 (live, subadult; leg. HBS). D) North Bohemia, Liberec, Ještěd Mt., southwestern slope, about 980 m NN, quartzite block field (all specimens caught alive), 1 ♂ (subadult), 5 ♀♀ (4 adult, 1 as 3rd instar), 31.7.2003 (leg. V. Růžička & HBS; CHBS).

USSR, Siberia (sub *W. longicornis*): 1 ♂, 1 ♀ (Paratypes; Krasnoyarsk Area, Yenisey River, Mirnoye, in stack of fire logging, 6.9.1979, leg. K. ESKOV; SMF 32149).

Methods

Ex ovo-rearing: Reproductive females from the wild and breeding pairs were kept in slightly conical 500 ml plastic tubs containing a plaster-charcoal layer with a piece of quartzite rock. The plaster layer was mois-

tened weekly with a few drops of water. Spiderlings hatched from egg sacs were kept separately in small glass vessels (25 ml; 1 cm charcoal-plaster layer). Pieces of perforated airtight film were used to cover vessels and tubs. All mated females and juveniles beyond moulting were fed (almost) daily with arthropodous (spring-summer) and symphypleonous (autumn-winter) Collembola. The size of the prey did not considerably exceed the spiders individual body length. Keeping and rearing were maintained in the dark under normal room conditions (Temperature 15–22°C).

Measurements: The growth of the juvenile spiders was monitored on an (almost) daily basis by recordings of body dimensions of live specimens, hanging upside down in their sheet webs (stereoscopic binocular microscope, magnification x40 to x80, calibrated ocular micrometer). The following characters were measured: a) sternum width between coxae II, b) maximum breadth of opisthosoma, c) total body length and d) leg span. The leg span was measured only in undisturbed, relaxedly resting specimens.

Courtship, mating behaviour: All observations were made in September and October at about 19 °C between 8:00–10:00 p.m., using a stereoscopic microscope (magnification x10) at half-light conditions. Recently moulted females were allowed to inhabit a 500 ml plastic tub (see above) for at least 2 days, to establish their sheet web. Then single males were introduced and constant observations started until successful mating had occurred.

Developmental stages: For both sexes a certain number of successive instars from ex ovo-rearings were fixed in 70 % ethanol. Specimens just before, or shortly after a moult were not considered. Lateral prosoma views of all instars were drawn following dissection of the legs between coxae and femora.

Abbreviations: E = embolic division; ED = entrance duct; Emerg = emergence from egg sac; Fe = femur; L/TL = length/total body length; Lc₁/Lc₂ = main/secondary branch of lamella characteristic; ♂/♀ = male/female; OpW = opisthosoma width; PME = posterior median eyes; Prs = prosoma; R = radix;

Rc₁/Rc₂ = receptacula; SteW = sternum width; T = tegulum; T₁ = terminal apophysis of tegulum; Ta = tarsus; W = width; e.o. = ex ovo; d = dorsal; pl = prolateral; rl = retrolateral; v = ventral; s.d. = standard deviation; SMF = Senckenberg Museum Frankfurt; CHBS, CKTh, CVR = author's collection, coll. K. THALER, coll. V. RŮŽIČKA.

Measures: Linear measures, if not otherwise indicated, are in mm.

Results

Geographic variation and description of a new subspecies

Geographic variation: The study of the geographic variation of taxonomic characters in *W. uralensis* is exclusively based on specimens, which were caught in the wild. The respective descriptions of differing characters are purposefully brief and provided in tabulated form for clarity. In the three-columned table (see below) the spiders are distinguished according to their geographical origins. The sequence is from East (Siberia; ** = geogr. position of the city of Krasnoyarsk) to West (Germany). Corresponding

characters in European populations (Czech Republic, Germany) are indicated by a local cancellation of the column subdivision.

The designation of the male palpal sclerites is according to ESKOV (1986). In all data on body measures and tibial spinulation of specimens from the Siberian main area, data from ESKOV (1986) have also been included (Symbol: *). Measurements of specimens from European populations are given as mean and range (in brackets). Tibia spine numbers refer to the normal case, assigned numbers in brackets inform about 1–2 cases of observed exceptions.

Description of a new subspecies: Disregarding some few minor differences, the comparison of taxonomic characters shows that the Central European specimens of *W. uralensis* are clearly distinct, when compared with the Siberian paratypes. Subject to further investigations, the observed differences in somatic characters are here regarded as the expression of geographic variation (see Discussion). Hence, all currently known European *W. uralensis* populations are assigned to a separate, allopatric taxon on a subspecific level.

USSR, Siberia, Krasnoyarsk Area 55°55'N, 93°00'E** 1 ♂, 1 ♀ (Paratypes)	Czech Republic 50°43'–50°45'N, 14°17'–15°49'E 4 ♂, 7 ♀	Germany 51°47'N, 10°27'E 14 ♂, 14 ♀
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General Appearance

Comparatively dainty spiders: TL _{MF} * = 2.10–2.20 PrsW _{MF} * = 0.80–0.83 / 0.74–0.76 PrsL _{MF} * = 0.93–0.95 / 0.87–0.90 Legs/femora not noticeably long: Leg I/IV L _m = 5.6/5.5 x PrsW Leg I/IV L _r = 5.5/5.4 x PrsW Fe I L _m = 1.44 x PrsW (1.50*) Fe I L _w = 1.46 x PrsW (1.53*)	Comparatively big, robust spiders: TL _{MF} = 2.40 (2.04–2.85) / 2.36 (2.03–2.90) PrsW _{MF} = 0.94 (0.86–1.02) / 0.84 (0.78–0.89) PrsL _{MF} = 1.14 (1.05–1.30) / 1.02 (0.94–1.10) Legs/femora noticeably long: Leg I/IV L _m = 6.9/6.8 x PrsW Leg I/IV L _r = 6.4/6.6 x PrsW Fe I L _m = 1.79 x PrsW (1.68–1.89) Fe I L _w = 1.70 x PrsW (1.63–1.81)
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Tibia spines: males

d	pl	rl	v	d	pl	rl	v
Ti I 2	0	0	0	Ti I 2 (3, 4)	1 (0)	1 (0)	1–3
Ti II 2	0	1	0	Ti II 2	0–1 (2)	1	1–2 (0, 3)
Ti III 2	0	0	0	Ti III 2	0 (1)	0–1	0–2
Ti IV 2	0	0	0	Ti IV 2	0–1 (3)	0–1 (2)	0–2

Tibia spines: females

d	pl	rl	v	d	pl	rl	v
Ti I 2	1	1	0	Ti I 2	1 (2)	1 (2)	1–3 (4)
Ti II 2	0	1	0	Ti II 2	0–1	1	1–2
Ti III 2	0	0	0	Ti III 2	0	0–1	0–2
Ti IV 2	0	0	0	Ti IV 2	0–1	0–1	0–1 (2)

USSR, Siberia, Krasnoyarsk Area 55°55'N, 93°00'E** 1 ♂, 1 ♀ (Paratypes)	Czech Republic 50°43'-50°45'N, 14°17'-15°49'E 4 ♂♂, 7 ♀♀	Germany 51°47'N, 10°27'E 14 ♂♂, 14 ♀♀
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Male Prosoma

Prosoma, when seen from above, well convex, slightly longer than wide, with widest part in prosoma middle (Fig. 9).	Prosoma, when seen from above, clearly longer than wide, rather pear-shaped, with widest part in proximal prosoma third (Fig. 12).
Postocular horn short, conical, straight, distally not curved (Fig. 10), not projecting the anterior margin of PME when viewed from above (Fig. 9). The robust terminal seta directed forward and upward at an angle of approximately 30°.	Postocular horn long, distally curved (Fig. 22, 11) reaching the anterior margin of (Czech specimens) or clearly projecting the PME (German specimens) (Fig. 12). The robust terminal seta either parallel to body axis or slightly pointing downwards (Fig. 22, 11). Fig. 11 shows head region of a single malformed male, having a double seta (ex ovo-rearing 2000, Harz Mts.).
Posterior prosoma comparatively short, ending blunt and rounded. Head region not especially pronounced (Fig. 10). Except head region, prosoma without bristles or short spines.	Posterior prosoma noticeably prolonged and ending flattened. Head region distinctly set off against proximal prosoma half (Fig. 22). Prosoma flanks with numerous short spines, often in rows (Fig. 22).

Male palp

Lc main branch (Lc.) narrow and ribbon-like, distally gradually tapering. Upper margin almost straight, both lateral terminal teeth short and unequal in size (Fig. 1).	Lc main branch similar to specimens from Harz Mts., but upper terminal tooth small, lower terminal tooth fairly rough and cone-shaped (Fig. 15).	Lc main branch rather wedge-shaped, distally rapidly tapering. Upper margin distinctly curved, both lateral terminal teeth slim, comparatively long and almost equal in size (Fig. 5, 14).
Maximum ♀ : L = 1 : 8.2	Maximum ♀ : L = 1 : 5.5	Maximum ♀ : L = 1 : 5.6–6.1
Proximal cymbium claw curved almost equally sickle-like (Fig. 2)	Proximal cymbium claw basally almost straight, only terminal half slightly curved (Fig. 6)	
Basic embolic part a semi-circular plate, the protruding embolic spur slim and long (Fig. 2).	Basic embolic part a trapezoidal plate, the protruding embolic spur claw-like, proximal part widened (Fig. 6).	
Rounded terminal radix corners (R) smaller than basic, semi-circular embolic part (Fig. 2).	Rounded terminal radix corners almost equal in size with basic, trapezoidal embolic part (Fig. 6)	

Epigyne and Vulva

Epigyne subconical, roughly heart-shaped, centre part of anterior margin with flat convex projection, lateral margins almost straight or very slightly concave (Fig. 3).	Epigyne similar to specimens from Harz Mts., but centre part of anterior margin with strong convex projection (Fig. 16).	Epigyne subconical, slightly reminding of a bike saddle, centre part of anterior margin almost straight, lateral margins clearly concave (Fig. 7, 13).
Entrance ducts starting anteriorly from copulatory opening almost right-angled (Fig. 4).	Entrance ducts starting anteriorly from copulatory opening oblique (Fig. 8).	

Wubanoidea uralensis lithodytes,
new subspecies

Types: Holotype ♂, Allotype ♀, trap catches, 27.6.–20.7.1999, Northwest Germany, Lower Saxony, Harz Mts., Acker-Bruchberg mountain range south-west of Altenau, open extensive quartzite block field (51°47' N, 10°27' E), leg. HBS, deposited in the Museum of Natural History, Humboldt University, Berlin (ZMB 35218). Paratypes:

same locality, 1 ♂, 1 ♀ 22.4.–7.6.2002, 1 ♀ 22.9.1999, 1 ♂ 24.9.2001, leg. HBS, for the time being retained in CHBS.

Etymology: Greek: "lith-" = rock, stone; "dyt-" = diver. The subspecific epithet alludes to the exclusive habitat of all currently known populations in Europe (see Introduction).

The subspecific status of specimens from European populations is founded on the allo-

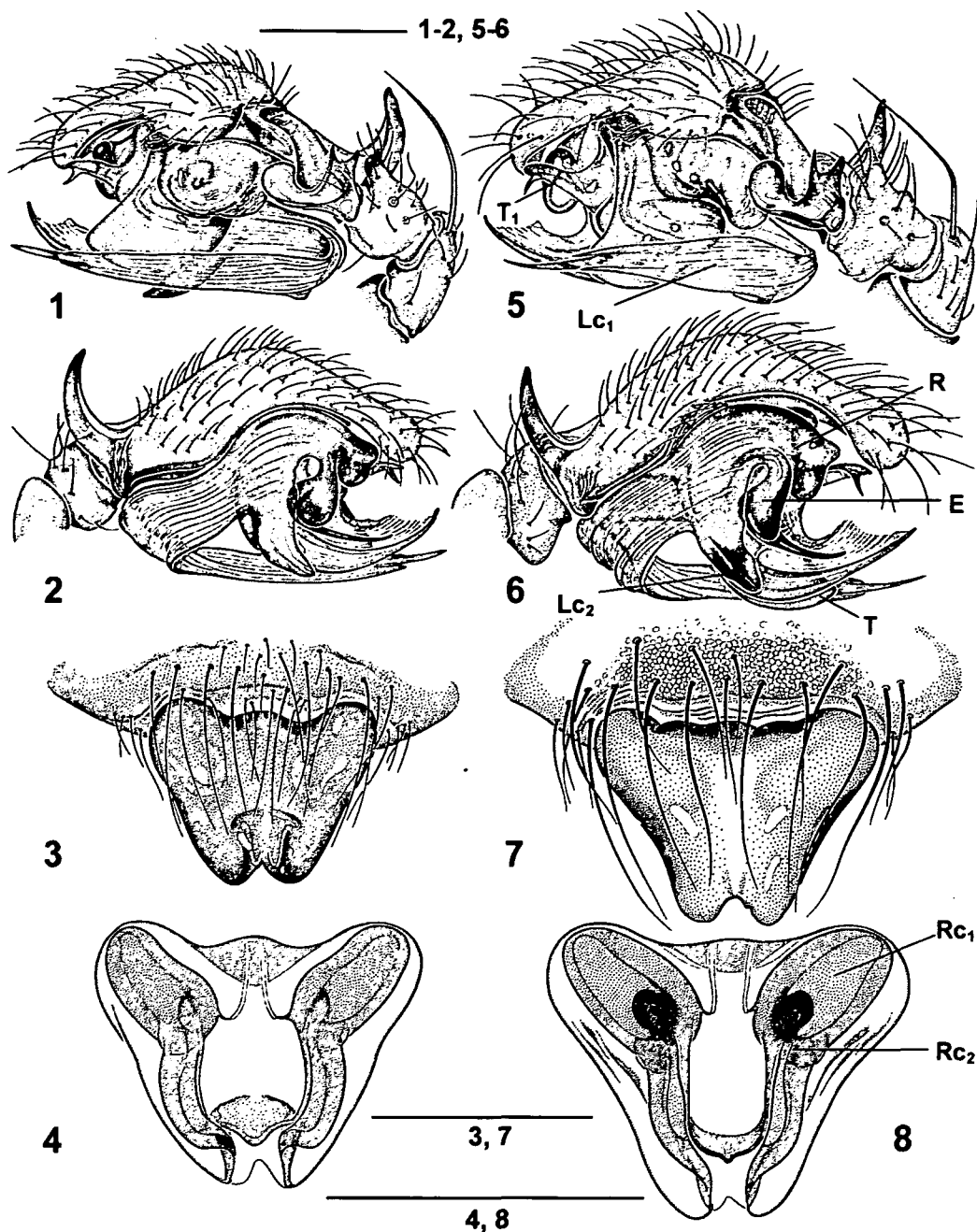


Fig. 1-8: *Wubanoidea uralensis uralensis* (Siberian paratypes; 1-4) and *W. u. lithodytes* nov. subsp. (Harz Mts.; 5-8). 1: Left male palpus, lateral view. 2: ditto, mesal view. 3: Epigyne. 4: Vulva, cleared, ventral view. 5: Left male palpus, lateral view. 6: ditto, mesal view. 7: Epigyne. 8: Vulva, cleared, ventral view. Scale lines = 0.25 mm.

metric differences (leg lengths; see above), the presence of ventral tibia spines at least on legs I-II (see above), prosoma characters in males (Fig. 12, 22 versus 9-10), and on characters of the male and female copulatory organs (Fig. 5-8, 13-16 versus 1-4).

Courtship and mating behaviour

Courting and mating behaviour was observed in five *Wubanoidea* couples (Harz Mts.). Spiders from the wild (caught as juveniles) and/or specimens from ex ovo-rearings were brought together some days after their final ecdysis. Usually copulation was

noticed 45-75 minutes after the male came in contact with the female web.

Courtship: Once in contact with the web of a female, the male of *W. uralensis* is mostly motionless for several minutes. Then it starts jiggling the abdomen impulsively and rhythmically, and enters the web in a creeping way (Fig. 46). Soon the male displays also additional impulsive and sudden body movements. The web vibrates markedly. Up to five jig impulses are followed by a short break, then the jiggling of the abdomen starts anew. Stridulation begins, the

Fig. 9–16: *Wubanoides uralensis uralensis* (Siberian paratype; 9, 10) and *W. u. lithodytes* (Germany, Harz Mts.: 11–14; Czech Republic: 15, 16).

9: Male prosoma, dorsally,

10: ditto, laterally.

11: Head region of malformed male with double seta, lateral view.

12: Prosoma, dorsal view.

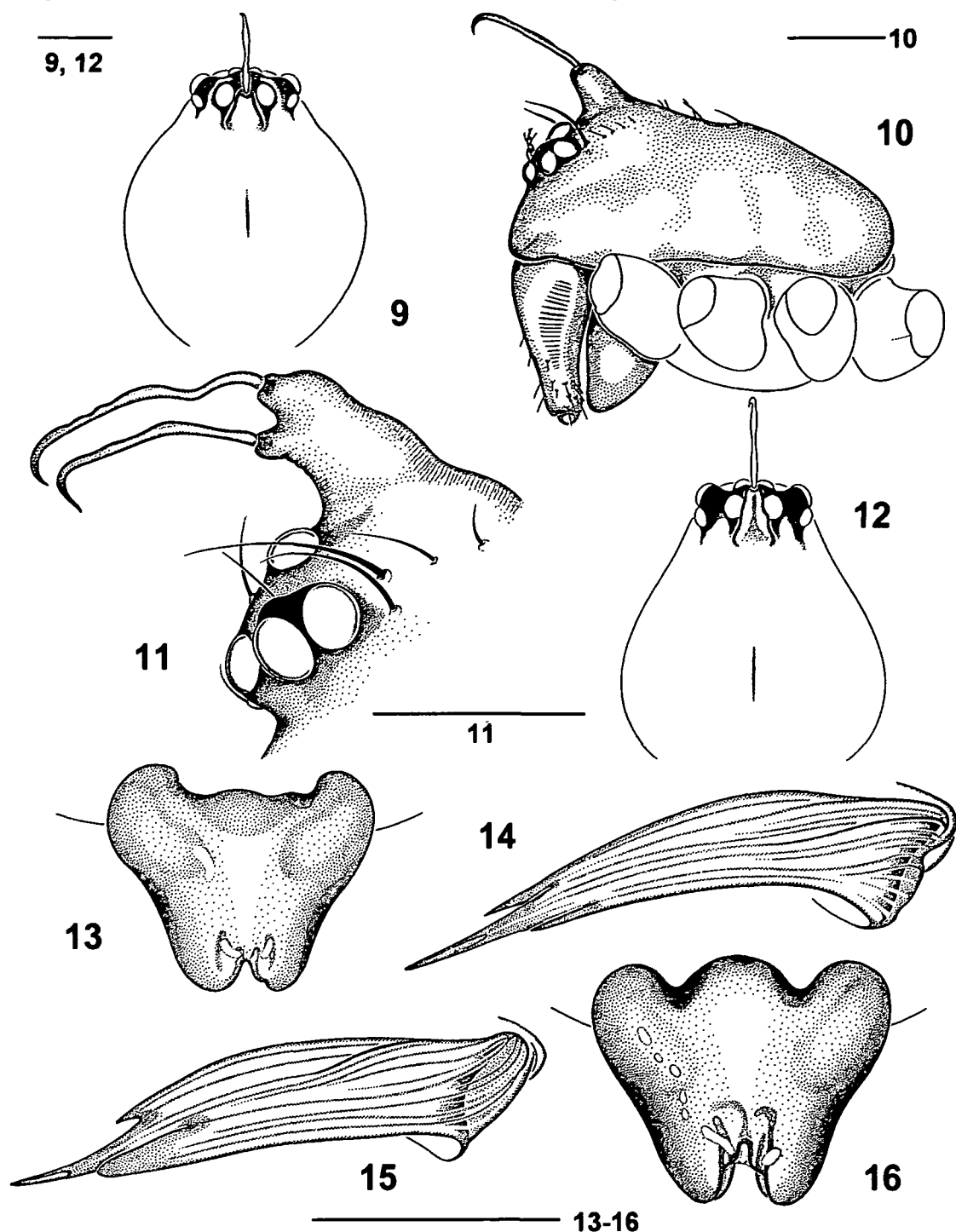
13: Epigyne.

14: Lamella characteristica, left palp, laterally.

15: Lamella characteristica, left palp, laterally (Sněžka Mt.).

16: Epigyne (Králický Sněžník Mt.).

Scale lines = 0.25 mm.



palps are moved up and down alternately. The stridulatory bristle, mesally surmounted on a small tubercle of the basal palpal femur end, is scraped along the stridulatory ridges laterally of the cheliceral bases. The resulting vibrations of the palpal bulbi are clearly visible. Unmated females react either passively, or rush towards the intruder. Very offensive females try to repulse the male with their forelegs. In this case the male escapes from the web, but soon starts to perform the

courtship display again. When there are no further acts of aggression on part of the female, the male usually approaches the female directly. Sometimes even foreleg contacts can be observed. The male now starts to run around the female in curves, dabbing its opisthosoma tip regularly onto the web, attaching its own silk threads.

The male excitation obviously increases, sudden body movements and opisthosoma jiggling are carried out at increasingly

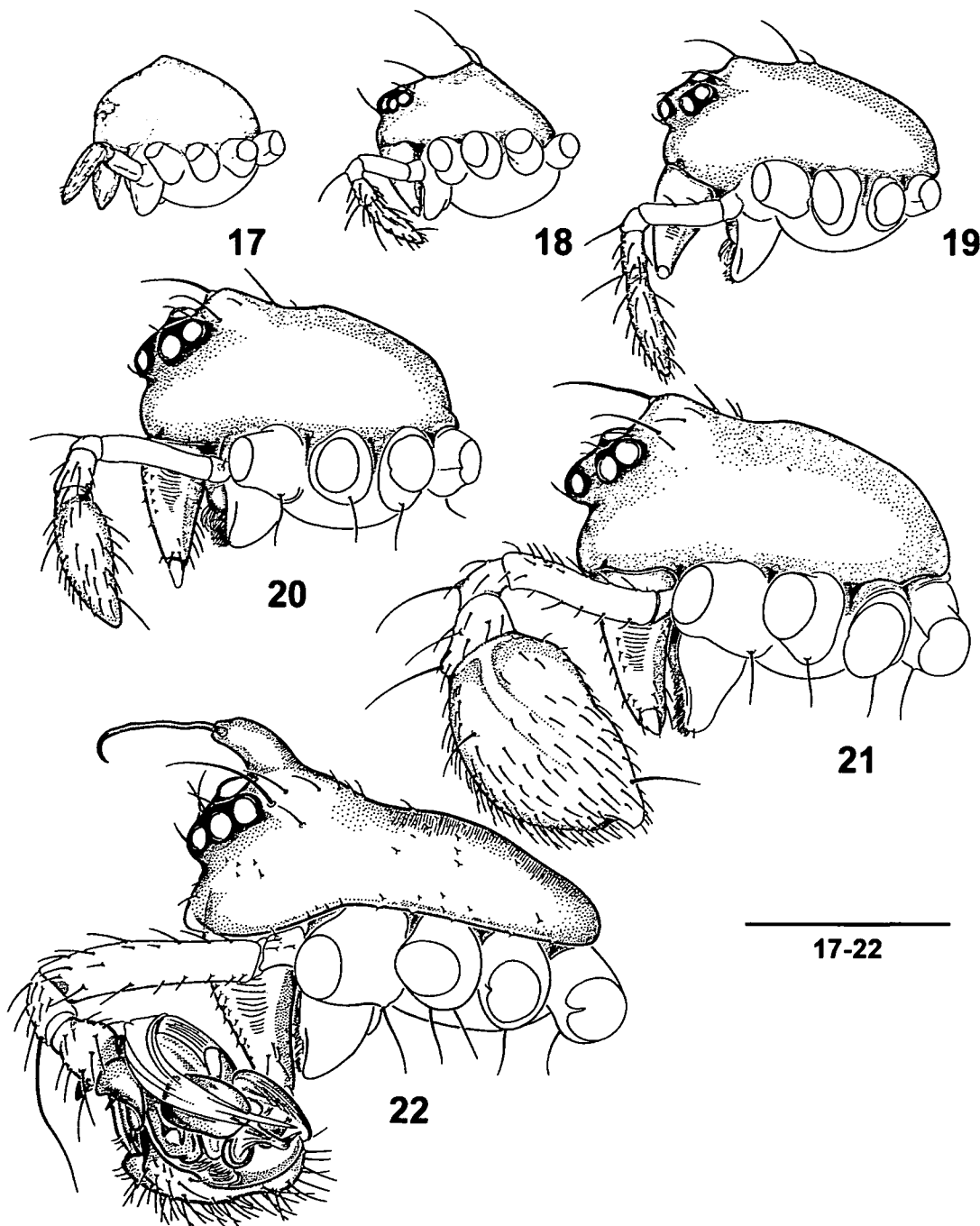


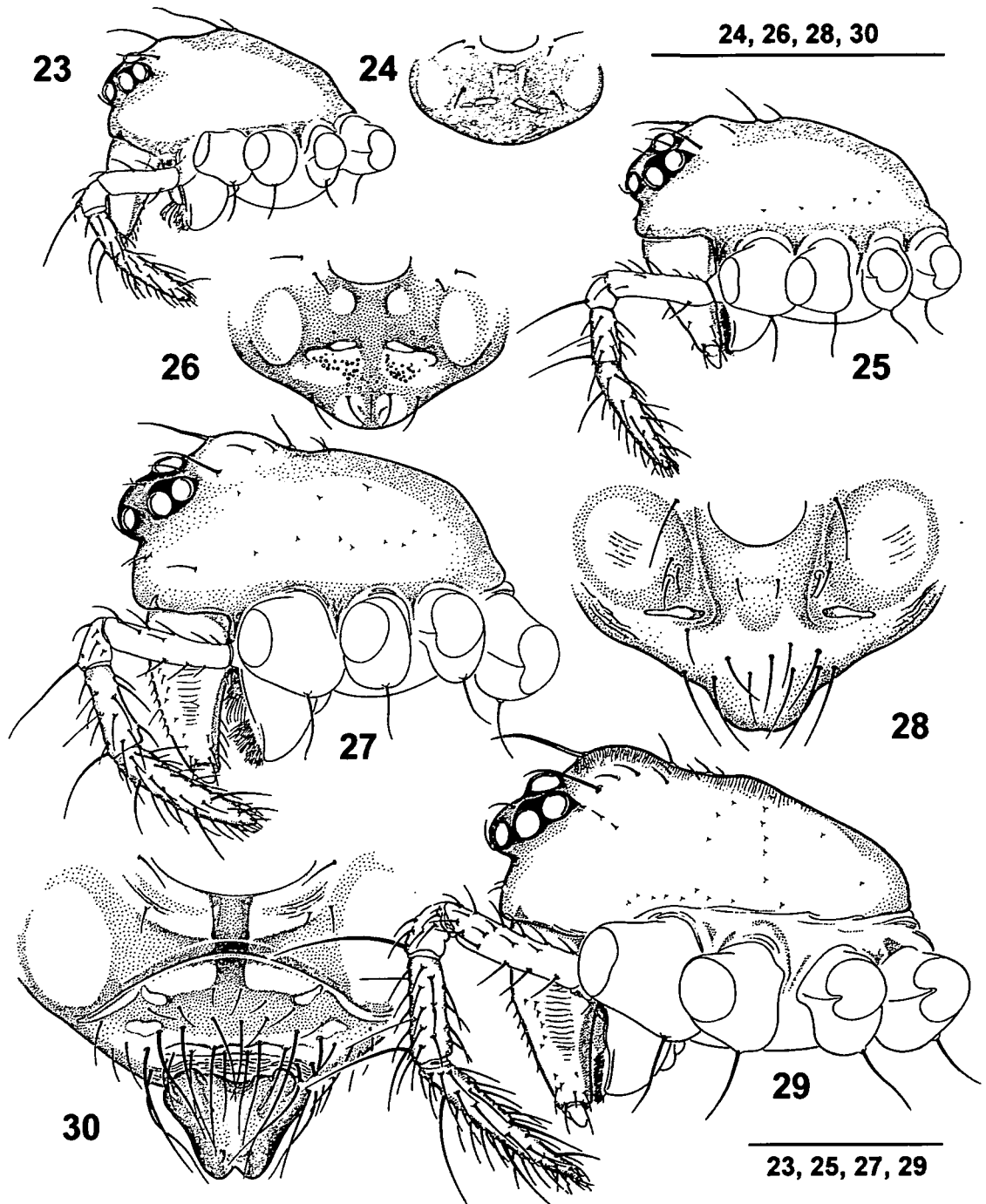
Fig. 17–22:
Wubanoidea uralensis
lithodytes (ex ovo-
rearing; Harz Mts.).
Postembryonic
development of
males, lateral
prosoma views, legs
dissected off.
17: First post-
embryonic instar (sex
unknown).
18: Second instar (=
first free instar; sex
unknown).
19: Third instar male.
20: Fourth instar male.
21: Fifth instar male
(subadult).
22: Sixth instar male
(adult). Scale line =
0.5 mm.

shorter intervals. Palpal stridulation activity now resembles a drumming. Phases of jiggling now last for 30–70 seconds and culminate with a 9–15 second stridulation. During stridulatory activity, the male takes up a long-legged posture below the web surface, but at the cessation of the stridulation the leg positions are re-arranged. Each phase of courting is followed by a break of up to 140 seconds. The female is now frequently surrounded completely by the male, which continues attaching its own threads to the web. On this occasion the male usually

starts to work on its palp tips alternately with the chelicerae.

Sperm web construction: The male bites a hole into the female's web, having a diameter of about 1.5–2 body lengths. With nervous, convulsive movements it builds a sperm web inside the opening within some few seconds (Fig. 47). In the course of sperm web construction the male climbs up several times to the sheet web surface and deposits a droplet of sperm from the epigastric genital opening onto its sperm web. The tiny sperm web is irregularly triangular (e.g.

Fig. 23–30:
Wubanooides uralensis
lithodytes (ex ovo-
 rearing; Harz Mts.).
 Postembryonic
 development of
 females, lateral
 prosoma views, legs
 dissected off.
 23: Third instar.
 24: Ditto, epigynal
 region.
 25: Fourth instar.
 26: Ditto, epigynal
 region.
 27: Fifth instar
 (subadult).
 28: Ditto, epigynal
 region.
 29: Sixth instar (adult).
 30: Ditto, epigyne.
 Scale line = 0.5 mm.



1.6 x 1.3 x 0.8 mm), and is tensed up with three silk threads. Sperm reception takes place while the male sits below the web surface. Both palp tips are brought up alternately to the sperm web from above in a rather rapid sequence (Fig. 48). A male is capable of constructing a second sperm web in the course of courtship.

Mating: A short time after sperm reception the male starts courting again. The female is now pressurized severely by the male from the front and laterally, using tarsi and

metatarsi of the forelegs. After some initial repulsive movements, the female raises both frontal leg pairs and remains in this position. The soft, flexible basal part of the epigyne becomes expanded and resembles a whitish proboscis (Fig. 49). Standing head to head, the male now pushes impetuously forward with its prosoma underneath the female's prosoma. On this occasion the female fixes the male postocular protuberance between her chelicerae (Fig. 50). Doing this, the robust male terminal seta obviously

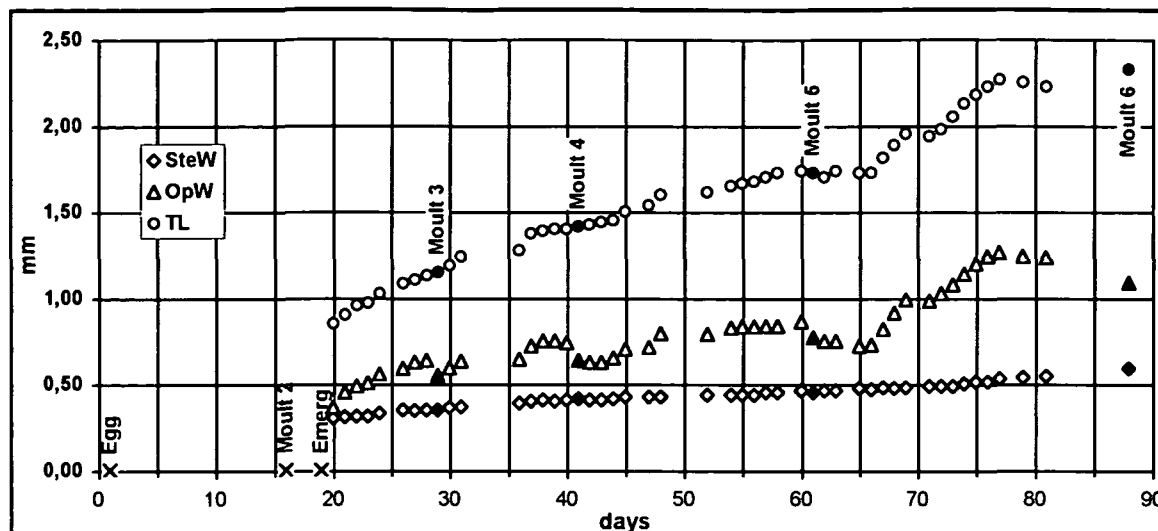


Fig. 53: *Wubanoidea uralensis lithodytes* – Course of the individual development in a female from the egg (29 August) to the adult (24 November 1999). Ex ovo-rearing. SteW = sternum width; OpW = opisthosoma width; TL = total body length; Emerg = emergence from egg sac.

functions as a guiding device. Almost contemporaneously the alternating insertion of the male's palps happens and the expansion of the haematodochae become visible (Fig. 51). The observed copulations were rather short and lasted only 20–120 seconds. The female partner initiates the separation and leaves the male. No multiple matings could be observed in females, but males can successfully inseminate more than one female. Obviously the period after final ecdysis, in which females are willing to mate (one or two weeks), ends with the start of the egg maturation process.

Postembryonic development

All body measures of the free instars exclusively refer to specimens shortly after a successful moult, before starting/continuing to trap prey again. A distinction of the body measures between both sexes is neglected in the following, since no clear or distinct differences were found shortly after a moult.

The free instars of development need four moults to reach adulthood. Both sexes can be distinguished for the first time in the second free instar by the shape of their palp tips (Fig. 19 versus 23). According to 169 ex ovo-specimens from 20 egg sacs, the sex ratio in *W. uralensis lithodytes* appears slightly skewed in favour of the male sex (1 : 0.8; males = 94, females 75). Details on the duration of the entire postembryonic development are given in connection with the adult stage (5th free instar).

Egg sac and egg (Fig. 33): The data basis for measurements and observations con-

sisted of a total of 25 egg sacs from eight mated females and, additionally, 2 egg sacs from the wild. The spiders were able to establish up to seven egg sacs (mean = 3.1; range = 1 to 7). They were built mainly in small rock depressions, or on the plaster ground of the plastic tubs. Establishment of the first egg sac after mating or after the production of a prior egg sac, took 9.9 days on average (s.d. = 4.0; range = 3 to 30). The egg sacs are silky white. The total length of one measured egg sac including of its loose peripheral silk layer was 6.8 mm. The rather dense padded central part, containing the egg bale was about 1.7 mm in diameter.

The egg numbers ranged from seven to 14 (mean = 10.2, s.d. = 2.0). Both egg sacs, which were found in the wild (11.6.2001, 20.8.2002), contained nine eggs each. The mean egg diameter was 0.54 mm ($n = 24$; s.d. = 0.03, range = 0.50 to 0.60). The eggs are spherical, pale yellowish in colour, and stick together in a bale with the shape of a mulberry. The diameter of two measured egg bales was about 1.3 mm.

First postembryonic instar (Fig. 17, 34): 10–12 days after oviposition and 2–3 days before hatching, the egg becomes elongated, the prosoma and appendages of the embryo become visible through the silk layer of the egg sac. 13.5 days, on average, after egg sac establishment the eggs hatch ($n = 5$ egg sacs; range = 12–15 days). It was not observed if the covers of the egg (chorion and vitelline membrane) were broken and shed together with the embryonic cuticle, as it has been reported by other investigators (e.g.

GALIANO 1991, GALIANO & GOLOBOFF 1996). The shedding of the embryonic cuticle would be the first true moult. On the assumption, that such a moult also exists in *Wubanoidea*, the incomplete instar, which left the egg and remained in the egg sac, is here regarded as the first postembryonic instar.

The hatchlings of the first postembryonic instar (total length: 0.77–0.80, $n = 3$) are covered by a hairless cuticle, except for the distal part of the palps, where some short bristles exist. The pale yellowish hatchlings are eyeless and show a characteristic dorsal elevation. Tarsi and metatarsi of all limbs are still joined, cheliceral claws are not visible. Eyes and hairs of the developing second instar show through the cuticle only shortly before the second moult. In most cases the second moult occurred three days after leaving the egg.

Second instar (1st free instar; Fig. 18, 35): The second postembryonic instar is the first free instar. The first free instar spiderlings ($n = 180$) left the egg sac at the earliest eight days after egg sac establishment (mean = 18.3 days, s.d. = 4.1, range = 8 to 23) and 2–3 days after the second moult. They show a characteristic dorsal elevation with a long bristle. A distinction of both sexes was not yet possible at this stage. After leaving the egg sac, the spiderlings disperse and establish their first small sheet webs. It was found to be important that they have an opportunity to catch prey within three or four days at the latest. Otherwise the spiderlings frail and become too weak for a successful hunt.

Colour: Sternum greyish yellow. Opisthosoma ventrally greyish amber-coloured, dorsally and laterally somewhat paler. Legs and palps whitish yellow, diaphanous. Prosoma dorsally light yellowish white and diaphanous pale greyish.

Total length ($n = 161$):
mean 0.86 (s.d. = 0.04; range = 0.77–0.96)
Opisthosoma width ($n = 149$):
mean 0.35 (s.d. = 0.04; range = 0.29–0.48)
Sternum width ($n = 151$):
mean 0.29 (s.d. = 0.01; range = 0.27–0.33)
Leg span (Ta I–Ta IV; $n = 10$):
mean 2.15 (s.d. = 0.12; range = 1.88–2.30)

Third instar (2nd free instar; Fig. 19, 23, 36): In the second free instar the distinction of both sexes becomes possible for the first time. The distal palpus section of early males is, in contrast to early females, widest in the middle (Fig. 19 versus 23). The prosoma of early males shows a small postocular tubercle, surmounted by a slightly curved bristle. In early females this tubercle is only indicated. The initial stage of the epigynal development is characterized by a slight protuberance of the upper margin of the epigastric furrow (Fig. 24).

Colour: ♂/♀: Sternum anthracite grey, blackish granulated. Opisthosoma ventrally pale reddish brown, dorsally somewhat darker. Prosoma (dorsally), legs, palps and basic part of chelicerae light whitish grey, later becoming yellowish.

Total length ($n = 164$):
mean 1.17 (s.d. = 0.06; range = 1.03–1.34)
Opisthosoma width ($n = 161$):
mean 0.54 (s.d. = 0.05; range = 0.42–0.69)
Sternum width ($n = 162$):
mean 0.35 (s.d. = 0.01; range = 0.33–0.44)
Leg span (Ta I–Ta IV; $n = 57$):
mean 3.66 (s.d. = 0.27; range = 3.15–4.25)

Fourth instar (3rd free instar; Fig. 20, 25, 37): Young males now show a distinctly swollen terminal palpal section, with the widest part in the proximal third. The postocular tubercle is now characteristic and more prominent, its curved bristle is stronger. Fourth instar females exhibit a shallow postocular elevation. Their terminal palpus section is distally tapering gradually. In the epigynal region a rounded projection indicates further epigynal development (Fig. 26).

Colour: ♂/♀: Sternum grey, blackish granulated. Opisthosoma ventrally dark reddish brown to pale brown, dorsally and laterally pale whitish or yellowish brown. Prosoma dorsally yellowish brown to dull amber coloured, as are chelicerae, palps and legs. Spinnerets ventrally blackish.

Total length ($n = 138$):
mean 1.56 (s.d. = 0.09; range = 1.35–1.93)
Opisthosoma width ($n = 137$):
mean 0.72 (s.d. = 0.07; range = 0.60–1.03)
Sternum width ($n = 136$):
mean 0.43 (s.d. = 0.02; range = 0.38–0.48)

Leg span (Ta I–Ta IV; $n = 74$):

mean 5.34 (s.d. = 0.44; range = 4.20–6.40)

Fifth instar (4th free instar, subadult; Fig. 21, 27, 38, 40): Subadult *W. uralensis lithodytes* males are unmistakable by the combination of a very pronounced postocular elevation with a robust, forwardly directed, terminal seta, and strongly swollen palps (Fig. 21). The palp tips are extended into distinct, slightly curved, corners. Subadult females are as well distinctive. They show a pronounced, rounded postocular elevation with a forwardly directed bristle (Fig. 27). The shape of the strong projection above the epigastric furrow already indicates vaguely the appearance of the later epigyne (Fig. 28).

Colour: ♂/♀: Sternum grey, blackish granulated. Opisthosoma ventrally dark brown, dorsally dark hazel. Prosoma dorsally whitish yellow to amber coloured. Legs yellowish, ventrally darker.

Total length ($n = 93$):

mean 1.95 (s.d. = 0.12; range = 1.61–2.20)

Opisthosoma width ($n = 93$):

mean 0.86 (s.d. = 0.11; range = 0.64–1.50)

Sternum width ($n = 92$):

mean 0.51 (s.d. = 0.03; range = 0.44–0.58)

Leg span (Ta I–Ta IV; $n = 27$):

mean 7.23 (s.d. = 0.62; range = 6.10–8.35)

Sixth instar (5th free instar, adult; Fig. 22, 29, 32, 39, 45, 52): For the description of male characters see Results. After leaving the egg sac, ex ovo-males reach the adult stage within 63 days on average ($n = 12$; s.d. = 11; range = 48–81). The course of the final shedding in a male is illustrated on Fig. 41–44. Mean life expectancy of adult ex ovo-males ($n = 13$) was found to be 127 days (s.d. = 84, range = 16–264). Inclusive of all free living juvenile stages of development (2nd to 5th instar), male spiders reached a maximum age of 317 days (mean = 194; s.d. = 78, range = 70–317).

The prosoma of adult females resembles that of the subadult female stage (5th instar), but the posterior prosoma part is distinctively sloped (Fig. 29). The characters of the epigyne (e.g., Fig. 30) and vulva have been described elsewhere. Ex ovo-females reached adulthood within 58 days on average ($n = 18$; s.d. = 13, range = 38–91). These data indicate a more rapid develop-

ment in the female sex. Adult ex ovo-females ($n = 19$) lived 203 days on average (s.d. = 84; range = 46–360). The complete lifespan inclusive of all free-living juvenile stages was 429 days at maximum (mean = 261; s.d. = 92, range = 94–429). Figure 53 illustrates the individual course of development from egg to adult stage for a female ex ovo-specimen. The mother spider (caught 20.7.1999, Harz Mts.) of this female established the egg sac on 29.8.1999. The final moult of her female descendant was on 24.11.99. This spider reached an age of 360 days and died on 18.11.2000.

Colour: ♂ (Fig. 32, 45): Sternum dark grey, blackish granulated. Opisthosoma ventrally blackish, dorsally whitish or yellowish brown, distal half sometimes with 4–5 grey horizontal stripes. Region above spinnerets creme-coloured. Prosoma dorsally whitish yellow to orange yellow. Legs orange yellow, ventrally slightly darkened. Cymbium blackish, bulbus/bulbus sclerites blackish red brown.

♀: Similar to male after final moult (Fig. 39), but later generally much darker (Fig. 52 versus 45). Epigyne dark reddish brown, cuticula very fine wrinkled.

Total length ($n = 65$):

mean 2.37 (s.d. = 0.14; range = 2.10–2.75)

Opisthosoma width ($n = 62$):

mean 1.04 (s.d. = 0.10; range = 0.79–1.29)

Sternum width ($n = 62$):

mean 0.61 (s.d. = 0.03; range = 0.56–0.69)

Leg span (Ta I–Ta IV; $n = 8$):

mean 9.63 (s.d. = 1.04; range = 8.20–11.0)

Preliminary notes on ecology: Trapping results (Germany: Harz Mts.) and finds by hand picking (Czech Republic: Ještěd Mt.) in extensive block field habitats likely indicate an aggregated distribution pattern in *W. uralensis lithodytes*. The spiders seem to settle in loose colonies. There are clear indications of a seasonal abundance of *W. u. lithodytes* individuals in the block field habitat (Harz Mts.). Between the end of September and mid May neither juvenile stages nor adults have been found in accessible depths of up to 2.1 m. Interim results covering an extended period of study with temperature data loggers in different block field depths, show that the mean daily tempera-

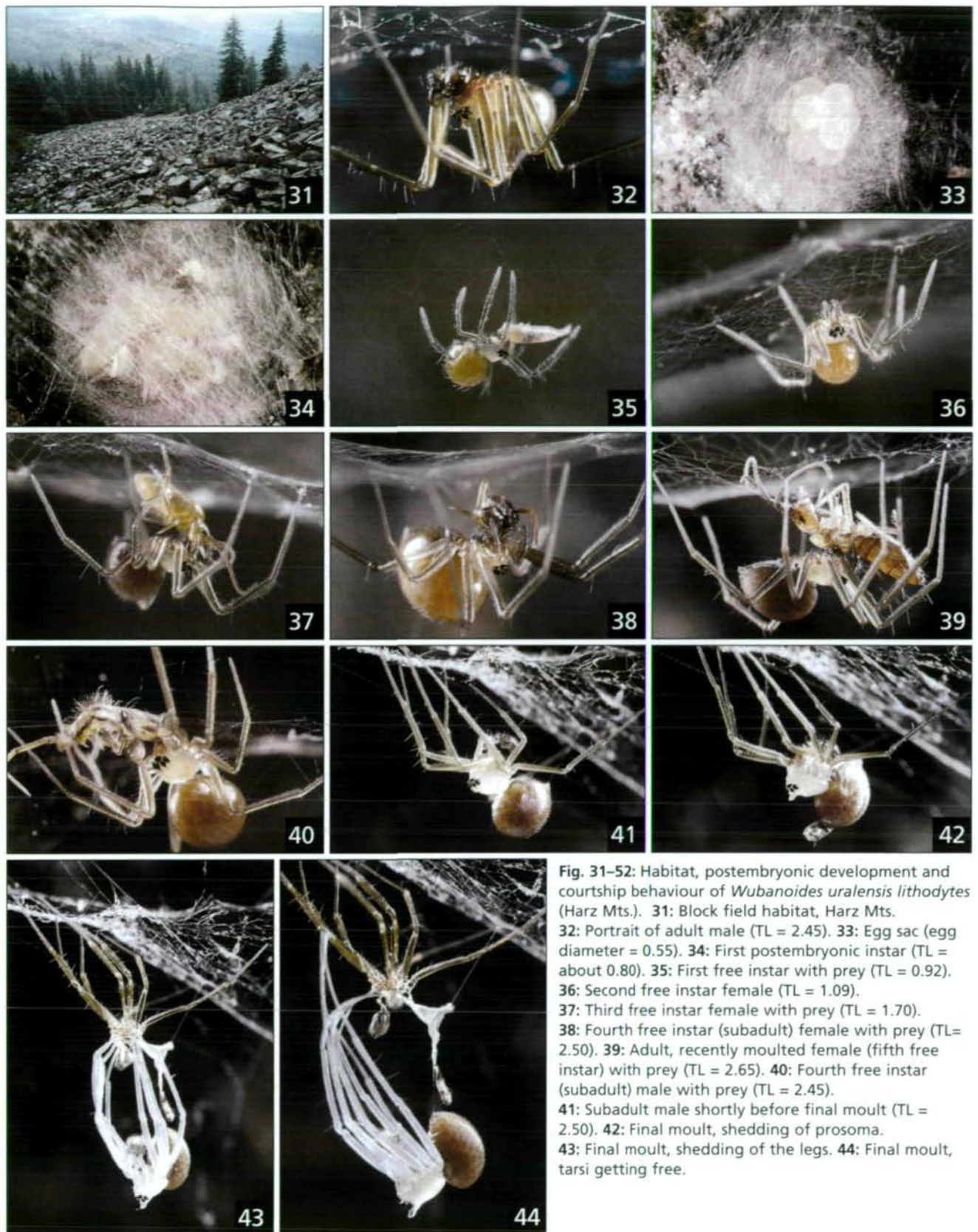


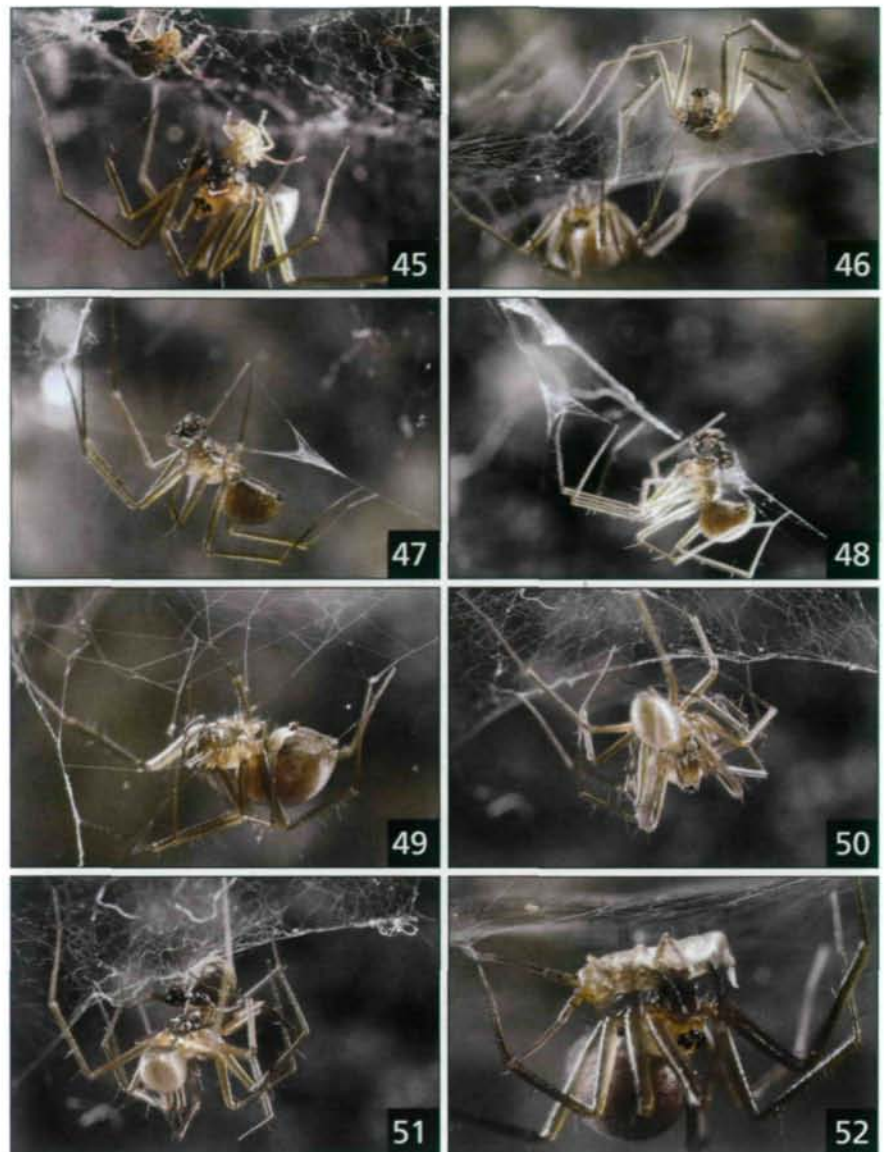
Fig. 31–52: Habitat, postembryonic development and courtship behaviour of *Wubanooides uralensis lithodytes* (Harz Mts.). 31: Block field habitat, Harz Mts. 32: Portrait of adult male (TL = 2.45). 33: Egg sac (egg diameter = 0.55). 34: First postembryonic instar (TL = about 0.80). 35: First free instar with prey (TL = 0.92). 36: Second free instar female (TL = 1.09). 37: Third free instar female with prey (TL = 1.70). 38: Fourth free instar (subadult) female with prey (TL = 2.50). 39: Adult, recently moulted female (fifth free instar) with prey (TL = 2.65). 40: Fourth free instar (subadult) male with prey (TL = 2.45). 41: Subadult male shortly before final moult (TL = 2.50). 42: Final moult, shedding of prosoma. 43: Final moult, shedding of the legs. 44: Final moult, tarsi getting free.

ture might be a crucial factor. After winter is over the first specimens were ascertained, when the mean daily temperature permanently exceeded 8 °C in 2.1 m below the block field surface again (1st third of May). Possibly individual spiders migrate into deeper zones in autumn. Under laboratory conditions no indication of an obligatory winter break was found. However, experiments in an unheated attic have shown that all instars, from egg to adult, can, in principle, winter over successfully. They withstood for a short time temperatures of down to -6 °C without any ill effect. In the field (Harz Mts.), a mated female has been found on 24 May at the earliest. Egg sacs, attached to traps, were discovered in 1–1.5 m below the surface on 11 June and 20 August.

In the course of ex ovo-rearing, each of the spiders ($n = 13$; 3 ♂♂, 10 ♀♀) consumed on average a prey biomass of 25 mg (arthropodous collembola) to reach adulthood (s.d. = 4.3; range 16–31). The respective mean number of caught collembolans – their size corresponding to the spiders individual body lengths – was 36 (s.d. = 4; range = 28–40).

Discussion

Wubanoidea uralensis shows a disjunct distribution pattern. The Siberian/North Asian main area (south-eastern coast of the Barents Sea up to east of Lake Baikal, and Mongolia; ESKOV 1986, 1994, ESKOV & MARUSIK 1992) is separated from the few known Central European locations by a wide gap, extending more than 2000 km (see maps in ESKOV & MARUSIK 1992; RŮŽIČKA & ZACHARDA 1994). Consequently the Central European area appears to represent the westernmost, tiny relict of a formerly continuous distribution. The results on geographic variation of taxonomic characters would support this assumption. The specimens from Central Europe are comparatively uniform in their taxonomic characters, but differ markedly from the Siberian paratypes in many aspects. This result may indicate an interrupted gene flow. The presently known Central European populations are hence seen and described here as subspecific, i.e., geographical modifications. Apart from different somatic characters, a



difference in habitat preferences is also obvious (see below).

All known occurrences of *W. u. lithodytes* are restricted to open extensive low mountain block field habitats, where the spiders exclusively inhabit the deep, subterranean cleft systems. The respective block field sites are never situated very far away from former, pleistocene glacier borders (RŮŽIČKA 1997; SCHIKORA 2001). According to the current opinion, block fields can only develop under periglacial conditions (MOLENDEN 1996; GUDE & MAUSBACHER 1999). The correlation of the known *W. uralensis lithodytes* habitats with former peripheral glacier zones might indicate in so far, that block fields may have functioned as refuges for *W. uralensis*, as it has been discussed by KROPP (1999) for the lycosid spider *Acantholycosa norvegica*. The

Fig. 31–52 (continued): 45: Adult male with prey (TL = 2.60). 46: Start of male courtship display, female in background. 47: Male with sperm web. 48: Male, taking up drop of sperm from its second sperm web. First web on the left. 49: Female with extended epigyne (TL = 2.60). 50: Initial phasis of mating. Female holds male terminal seta between her chelicerae. 51: Mating. Left male palpus is inserted, its haematodocha expanded. 52: Mated elder female with prey shortly before egg production.

possession of longer legs in *W. u. lithodytes* can possibly be rated as an adaptation to the block field habitat, as discussed for the linyphiid spider *Bathypantes similimus buchani* by RŮŽIČKA (1988). The recent findings in Central Europe could thus be regarded as relicts of former climatic periods ("glacial relicts"). This view is supported by the contrasting habitat preferences of *W. uralensis* within the North Asian main area. Here, the species was found above ground in a stack of fire logging, in *Alnus fruticosa* leaf litter of a rocky bank, and under stones of rocky banks or, respectively, of dry mountain tundra (ESKOV 1986).

Specimens from the 4 different Czech occurrences of *W. u. lithodytes* do not reveal considerable morphological differences in their copulatory organs. But compared with specimens from the westernmost known population in Germany (Harz Mts.), they are conspicuously separate in certain details (Fig. 15–16 versus 13–14), possibly suggesting restricted (or interrupted?) genetic relations. An experiment, carried out by the author, has shown that Czech and German specimens (♂: Krkonoše, Sněžka Mt., ♀: Harz Mts.) do interbreed successfully and produce viable offspring. These 1st generation descendants are unrestrictedly capable of reproduction, as it is indicated by a second viable offspring generation, which presently (1.2.2004) is in the subadult stage. Interbreeding experiments with specimens from Central Europe and the North Asian main area should also be suitable to elucidate their actual taxonomic relationship.

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Zusammenfassung

Wubanoidea uralensis (PAKHORUKOV, 1981) – Geografische Variation, Paarungsverhalten, postembryonale Entwicklung und Beschreibung einer neuen Unterart (Araneae, Linyphiidae). Für die Baldachinspinne *Wubanoidea uralensis* (PAKHORUKOV 1981) wird ein Überblick der geographischen Variation taxonomischer Merkmale vorgestellt. Das Hauptareal der Spinne ist der sibirisch-nordasiatische Raum, aus Mitteleuropa sind nur wenige disjunkte, relikartige Vorkommen bekannt. Europäische Tiere sind im Vergleich mit den sibirischen Paratypen taxonomisch distinkt. Auch zeigen sich unterschiedliche Lebensraumpräferenzen. Europäische Populationen werden deshalb einem eigenen Taxon auf Unterartniveau zugeordnet: *Wubanoidea uralensis lithodytes*. Erfolgreiche ex ovo-Aufzuchten ermöglichten die Beschreibung der Postembryonalentwicklung und des Paarungsverhaltens. Ergänzend werden Vorabinformationen zu ökologischen Aspekten gegeben.

References

- BUCHAR J. & V. RŮŽIČKA (2002): Catalogue of Spiders of the Czech Republic. — Peres Publishers, Praha: 1–351.
- ESKOV K.Y. (1986): On *Veles* Pakhorukov 1981 and *Wubanoidea* n. gen., two Siberian linyphiid genera (Arachnida: Araneae: Linyphiidae). — *Senckenbergiana biol.* 67 (1/3): 173–182.
- ESKOV K.Y. (1994): Catalogue of the linyphiid spiders of northern Asia (Arachnida, Araneae, Linyphiidae). — Pensoft Publishers, Sofia, Moscow: 1–144.
- ESKOV K.Y. & Y.M. MARUSIK (1992): On the mainly Siberian spider genera *Wubanoidea*, *Parawubanoidea* gen. n. and *Poecilometes* (Aranei Linyphiidae). — *Arthropoda Selecta* 1 (1): 21–38.
- GALIANO M.E. (1991): Postembryonic development in ten species of neotropical Salticidae (Araneae). — *Bull. Br. arachnol. Soc.* 8 (7): 209–218.
- GALIANO M.E. & P.A. GOLOBOFF (1996): Postembryonic development of *Actinopus* cf. *insignis* and *Diplura paraguayensis* (Araneae, Mygalomorphae). — *Bull. Br. arachnol. Soc.* 10 (4): 121–126.
- GUDE M. & R. MÄUSBACHER (1999): Zur Genese von Blockhalden. — *Decheniana-Beihefte* (Bonn) 37: 5–11.
- KROPF C. (1999): Zoogeografie der blockhaldenbe-

wohnenden Wolfspinne *Acantholycosa norvegica* (Thorell, 1872) (Arachnida, Araneae, Lycosidae). — Decheniana-Beihefte (Bonn) 37: 153–159.

MOLEND A R. (1996): Zoogeographische Bedeutung Kaltluft erzeugender Blockhalden im außer-alpinen Mitteleuropa: Untersuchungen an Arthropoda, insbesondere Coleoptera. — Verh. naturwiss. Ver. Hamburg (NF) 35: 5–93.

RŮŽIČKA V. (1988): Problems of *Bathyphantes eumenis* and its occurrence in Czechoslovakia (Araneae, Linyphiidae). — Věst. čs. Společ. zool. 52: 149–155.

RŮŽIČKA V. (1990): The spiders of stony debris. — Acta Zool. Fennica 190: 333–337.

RŮŽIČKA V. (1997): Spiders (Araneae) from boulder debris of Králický Sněžník and Hrubý Jeseník Mountains (Czech Republic). — Čas. Slez. Muz. Opava (A) 45 [1996]: 239–243

RŮŽIČKA V. & J. HAJER (1996): Spiders (Araneae) of stony debris in North Bohemia. — Arachnol. Mitt. 12: 46–56.

RŮŽIČKA V. & M. ZACHARDA (1994): Arthropoda of Stony Debris in the Krkonoše Mountains, Czech Republic. — Arctic Arctic and Alpine Research 26 (4): 332–338.

RŮŽIČKA V., BOHÁČ J., SYROVÁTKA O. & L. KLIMEŠ (1989): [Invertebrates from rock debris in north Bohemia (Araneae, Opiliones, Coleoptera, Dip-tera)]. — Sborn. Severočes. Muz.– Přír. Vědy, Liberec 17: 25–36 [In Czech with English summary].

SCHIKORA H.-B. (2001): Erster Nachweis der Gattung *Wubanoidea* Eskov, 1986 in Deutschland (Araneae, Linyphiidae). — Arachnol. Mitt. 21: 38–45.

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